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The hierarchy of directional interactions in visual motion processing

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Abstract

It is well known that context influences our perception of visual motion direction. For example, spatial and temporal context manipulations can be used to induce two well known motion illusions; direction repulsion and the direction aftereffect (DAE). Both result in inaccurate perception of direction when a moving pattern is either superimposed on (direction repulsion) or presented following adaptation to (DAE) another pattern moving in a different direction. Remarkable similarities in tuning characteristics suggest that common processes underlie the two illusions. What is not clear, however, is whether the processes driving the two illusions are expressions of the same or different neural substrates. Here we report two experiments demonstrating that direction repulsion and the DAE are in fact expressions of different neural substrates. Our strategy was to use each of the illusions to create a distorted perceptual representation upon which the mechanisms generating the other illusion could potentially operate. We found that the processes mediating direction repulsion did indeed access the distorted perceptual representation induced by the DAE. Conversely, the DAE was unaffected by direction repulsion. Thus parallels in perceptual phenomenology do not necessarily imply common neural substrates. Our results also demonstrate that the neural processes driving the DAE occur at an earlier stage of motion processing than those underlying direction repulsion.

1. Introduction

Coding of motion information by the visual system is a hierarchical process, with initial extraction of local motion measures being followed by "pooling" of these measures at a later global-processing stage (Adelson & Movshon, 1982; Albright, 1984; Huk & Heeger, 2002; Castelo-Branco *et al*, 2002). The considerable body of physiological and psychophysical data on the motion sub-system makes it an ideal substrate in which to study hierarchical processing. Consequently, there has been a recent focus on identifying where in the motion pathway various perceptual phenomena are mediated; such as motion transparency (Qian & Andersen, 1995, Castelo-Branco *et al*, 2002; Rosenberg *et al*, 2008), structure from motion (Andersen & Bradley, 1998), biological motion (Grèzes *et al*, 2001) as well as the DAE (Kohn & Movshon, 2004; Curran *et al*, 2006; Wiese & Wenderoth, 2007) and direction repulsion (Hiris & Blake, 1996; Kim & Wilson, 1997; Benton & Curran, 2003, Grunewald, 2004; Wiese & Wenderoth, 2007).

The DAE (Levinson & Sekuler, 1976) is induced through prolonged viewing of unidirectional motion (adaptor), followed by a brief presentation of a test stimulus whose direction differs from the adaptor by (say) 25º. Observers typically overestimate the adaptor-test direction difference by as much as 40º – 60º. Direction repulsion (Marshak & Sekuler, 1979) occurs when the two moving patterns are superimposed to form transparently moving surfaces. Again, the direction difference is over-estimated. Their similar tuning for speed (Benton & Curran, 2003; Curran *et al*, 2006) and direction (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979, Patterson & Becker, 1996; Schrater & Simoncelli, 1998; Braddick *et al*, 2002) reveals a common functional role of spatial and temporal contextual interactions in motion processing; a theme which is evident in other sensory coding (Schwartz & Dayan, 2007). This functional commonality between the DAE and direction repulsion suggests a common process, inhibition, drives both phenomena (Mather & Moulden, 1982). This cannot,

however, be taken as unequivocal evidence that the two phenomena are expressions of the same neuronal populations.

A number of studies have attempted to identify where in the motion processing pathway the DAE and direction repulsion occur. In the case of direction repulsion, a number of authors have proposed that the mechanism driving it occurs at the early, local-motion processing stages (Marshak & Sekuler, 1979; Hiris & Blake, 1996; Grunewald, 2004; Wiese & Wenderoth, 2007); while others have proposed it occurs at the later, global motion processing stages (Wilson & Kim, 1994; Kim & Wilson, 1996, 1997; Benton & Curran, 2003). These two stages of motion processing have been identified as occurring in area V1 and the human homolog of macaque MT/V5, respectively (Snowden, 1994; Huk & Heeger, 2002; Castelo-Branco *et al*, 2004). Again, in the case of the DAE, there is evidence supporting both a local (Kohn & Movshon, 2004; Curran *et al*, 2006a) and global motion processing (Kohn & Movshon, 2004; Wiese & Wenderoth, 2007) account. Because of these conflicting findings it is still unclear whether the DAE and direction repulsion are mediated by the same or different neuronal populations; and, if they are mediated by different populations, which occurs first in the motion pathway.

We report on two experiments that address these questions. The strategy of our experiments was to use each of the illusions to create a distorted perceptual representation upon which the mechanisms generating the other illusion could potentially operate. Our first experiment used the binary direction aftereffect (Curran *et al*, 2006b) to probe the neural mechanisms underlying these two phenomena. To induce the binary direction aftereffect (see Figure 1), observers adapt to a pattern containing superimposed fast (7º/s) and slow (2º/s) moving dots. The direction of the fast dots is offset 25º to one side (e.g. right) of vertical up, and the direction of the slow dots is offset 25º to the other side (left) of vertical. Following 30 seconds adaptation, observers are presented with a test stimulus containing the same fast and

slow dots, with all dots moving vertically upwards. However, the fast and slow dots appear to move to the left and right of vertical, respectively. The difference between the perceived directions of the two test speeds is a measure of the binary direction aftereffect. While previous investigations of this effect (Curran *et al*, 2006b) demonstrated that it comprises both DAE and direction repulsion components, the measurement paradigm employed did not distinguish whether these occur at the same or different stages of motion processing. We used an alternative paradigm with which to address this question in experiment 1. The results from this experiment were consistent with the DAE preceding direction repulsion in the motion processing hierarchy.

Experiment 2 involved observers adapting to a 'direction repulsion' stimulus before making direction judgments of a briefly-presented test stimulus. If (as suggested by the results of experiment 1) the DAE does precede direction repulsion, then perceived direction of the test stimulus should be distorted by the actual adaptor directions rather than its perceived directions. Again, our results were consistent with the DAE preceding direction repulsion. The combined results from these two experiments provide compelling evidence that the DAE occurs at an earlier stage of motion processing than direction repulsion and, consequently, that they involve different neural substrates.

2. Experiment 1: Direction adaptation affects direction repulsion

(a) *Methods*

(i) Observers

Six observers, the authors and three naïve, took part in the experiment. All observers had normal or corrected-to-normal visual acuity.

(ii) *Stimuli*

Experiment 1 was run in the Bristol and Belfast labs. Stimuli were random dot kinematograms (RDKs) presented within a circular aperture (6.2 deg^2) on a Sony GDM-F500R (Belfast) and a Sony CPD-500 (Bristol) monitor. Each dot was randomly assigned a polarity (black or white), with their mean luminance equal to the background luminance (40.01 cd/m^2). Dot density was 65 $dots/deg^2$. We chose viewing distances that would ensure that the stimuli subtended the same visual angle for each subject on the different experimental set-ups. Each monitor was driven by a Cambridge Research Systems VSG 2/5 graphics board at a framerate of 80Hz.

(iii) *Procedure*

During the initial motion adaptation phase (30s duration), observers were presented with a transparently moving random dot, mixed-speed stimulus in which 50% of the dots moved at 7 deg/s and the remaining dots moved at 2 deg/s. In addition to the difference in their speed, the dots also differed in their direction. Thus, the fast dots moved in a direction 25º to one side of vertical (upward), and the slow dots' direction was 25º to the other side of vertical. A central fixation spot was presented throughout the experiment. In the test phase immediately following adaptation, observers were presented again with a mixed-speed stimulus with each dot moving at either 7 or 2 deg/s. But this time all dots moved in the same direction – vertically up. The duration of the test stimulus was 400ms. A white line (length, 0.3º of visual angle) extended from the perimeter of the test stimulus. Observers were instructed to judge the direction of the dots (fast or slow) relative to the line segment. The line's orientation was chosen on each trial by an adaptive method-of-constants procedure (adaptive probit estimation), a method that dynamically updates the set of stimuli being presented depending on the observer's previous responses (Watt & Andrews, 1981; Treutwein, 1995). Line

orientations were selected to optimize the estimation of the "point of subjective equality" (PSE), in this case the orientation of the line when the dots were perceived to be moving in the direction the line was pointing.

Each block of trials comprised 64 test stimuli; test phases alternated with adaptation "top-up" phases of 5 seconds duration. Observers fixated a central fixation spot throughout. Each observer generated four psychometric functions per speed condition (7 and 2 deg/s test dots), with each psychometric function being derived from 64 trials. Prior to each block of trials, observers were informed of which speed set (slow or fast) they were to make direction judgments of.

A second experimental condition was run using a single-speed test stimulus, in which the test dot speed (2 or 7 deg/s) was randomly selected from trial to trial. Test dot density was the same as the equivalent speed set in the adaptor stimulus.

(b) Results

Figure 1 plots results of experiment 1. The binary direction aftereffect (grey bar) was consistently and significantly greater (paired t-test, 2-tailed, $t(5) = 3.01$, $p < 0.05$) than the sum of the DAEs obtained with the two single-speed test stimuli (black bar). It is important to note that the only difference between the conditions was the number of speeds in the test stimulus. The different aftereffect magnitudes suggest an additional interaction, in the form of direction repulsion, occurring with the two-speed test stimulus. To test this, observers judged the directions of a two-speed stimulus in which the slow and fast directions were offset to either side of vertical. These directions were determined by the DAEs from the earlier single-speed condition. Direction repulsion occurred for five of the six observers (white bar) and was significant across observers (one sample t-test, 2-tailed, $t(5) = 2.81$, $p < 0.05$), consistent with the hypothesis that the binary direction aftereffect is a combination of the DAE and

direction repulsion. The magnitudes of the DAE and direction repulsion suggest that the binary direction aftereffect results from a simple summing of the first two effects (although see Curran et al, 2006b, for a discussion of integrative processes underlying the binary direction aftereffect).

These results support the view that the direction aftereffect *precedes* direction repulsion. This becomes clear when considering the type of test stimulus used in the binary direction aftereffect condition. The test stimulus contained dots moving at one of two speeds, but all dots moved in the same direction. Note that direction repulsion effects only occur for patterns with two *different* motion directions. If presented without the prior adaptation, this mixed-speed test stimulus would not produce a direction repulsion effect. The adaptation resulted in speed-specific distorted representations of direction (DAE), such that the slow and fast test dots appeared to move in different directions. Our results suggest that the mechanisms underlying direction repulsion operated on these distorted representations. Of course this finding that the DAE precedes direction repulsion does not rule out the possibility that the two phenomena are the result of iterative processing occurring within the same neuronal population and, consequently, do not occur at different levels of the motion processing hierarchy.

If the direction aftereffect truly precedes direction repulsion in the motion processing hierarchy then adapting to a pattern in which direction repulsion occurs should result in a DAE driven by the actual, rather than the perceived, directions. Our next experiment tests whether this is the case.

3. Experiment 2: Direction repulsion does not affect direction adaptation

Experiment 2 was run in the Bristol and Sydney labs (the Sydney lab used a Sony G520 monitor and Cambridge Research Systems VSG 2/5 graphics board). In this experiment we had observers adapt to a bidirectional dot pattern which created a strong direction repulsion effect. Following adaptation observers judged the direction of a single-direction test stimulus. The key question here is which adaptor directions, perceived or actual, will induce a DAE in the test stimulus? If (as suggested by the results of experiment 1) the DAE precedes direction repulsion, then DAE measurements in this experiment will be determined by the adaptor's actual directions. Otherwise, they will be driven by its perceived directions.

(a) Methods

(i) Six observers, the authors and three naïve, took part in the experiment.

(ii) *Stimuli*

It was important that we used a stimulus which produced a large direction repulsion effect. Through piloting the experiment we found that Laplacian of Gaussian dot stimuli produced a larger effect than non-filtered dot stimuli. Adapting and test stimuli contained isotropic Laplacian of Gaussian (LOG) dots:

$$\nabla^2 G(x,y,\sigma) = \frac{1}{\sigma^2}\left(1 - \frac{x^2+y^2}{\sigma^2}\right)e^{-(x^2-y^2)/2\sigma^2}$$

with sd = 0.1º (Figure 2). Each micro-pattern had a peak spatial frequency of approximately 3.8 c/deg. At the start of each sequence, the polarity of each LOG function was randomly assigned. The contrast of the patterns was expressed as a proportional maximum deviation from the mean luminance and was 0.30. Mean luminance was 55 cd/m^2. The aperture edge

was blurred (with integral of Gaussian; sd = 0.1º). Stimuli were presented within a circular aperture (area = 19.63 deg^2), and micro-pattern density was 8.8 elements/deg^2.

(iii) *Procedure*

As a precursor to running the experiment proper, we measured the direction repulsion of two superimposed sets of dots whose directions differed by 60º. Both dot sets moved at the same speed (4 deg/s) and their directions were offset to the same side of vertical. Using a direction-judgment task we identified the directions of both dot sets when the dot set moving closest to vertical was *perceived* to be moving vertically up (Figure 2). Observers were then tested with a stimulus containing these two directions and, using the line orientation task of experiment 1, we identified the perceived direction of the set of dots moving further from vertical. The direction repulsion of each dot set varied across observers; for the dot set moving closest to vertical repulsion ranged from 8.34 - 11.56 degs, and ranged from 2.89 – 11.74 degs for the dot set moving further from vertical.

We now had the four direction parameters necessary for running the experiment – two actual directions and their perceived directions (Figure 2). In the 'bidirectional' condition observers adapted to an RDK stimulus containing two motion directions differing by 60º; the directions were individually tailored for each observer using the direction parameters obtained from the previous condition. Initial adaptation lasted 30 seconds and subsequent top-up adaptation phases lasted 5 seconds. The test stimulus (speed, 4 deg/s) contained dots moving in the direction half way between vertical up and the adapting direction closest to vertical up. The directional offset of the test stimulus from vertical was determined by each observer's repulsion measurements from the previous condition. The line orientation task was used to measure perceived direction of the test stimulus. We also measured the DAEs

induced by each of the actual and perceived adaptor directions individually, which were compared with the DAE from the bidirectional condition.

(b) Results

Figure 2 plots the DAE magnitudes obtained in the bidirectional condition (black squares) as well as the mean DAEs obtained using adaptors containing individual perceived directions (green triangles) and actual directions (blue triangles).

Across observers, the mean DAE to the bidirectional adapting stimulus was 4.21±0.31º. This value is closely predicted by the average of the DAEs induced by the two actual adaptor directions (5.03±0.25º; $t(5) = 2.10$; $p = 0.090$) – model 1. In contrast, it differs markedly from the average of the DAEs induced by the perceived directions (0.44±0.82º; $t(5) = 4.33$; $p = 0.008$) – model 2. A quantitative comparison of the measured likelihoods of these two models yields a Bayes Factor of 12.0, indicating that the data constitute strong evidence in favour of the hypothesis that the bidirectional DAE involves adaptation to the actual rather than the perceived directions of the component motions (Jeffreys, 1961).

4. Discussion

Schwartz *et al* (2007) highlight the tendency to treat temporal and spatial contextual effects separately, even when they reveal similar functionality and have a similar impact on vision. This observation applies to two well known visual illusions brought about by temporal and spatial contextual manipulation – direction repulsion and the DAE, respectively. We sought to determine whether there is any justification in treating these effects separately or whether they do, in fact, reflect activity of the same neuronal populations.

In experiment 1 we were able to induce direction repulsion in a test stimulus which would not normally exhibit spatial contextual effects without prior adaptation. Using an appropriate adaptor we were able to induce speed-specific direction aftereffects in opposing directions; this perceptual distortion was, in turn, operated upon by the mechanisms underlying spatial contextual effects to produce additional direction repulsion. These results are strongly suggestive of separate mechanisms driving the DAE and direction repulsion, and that mechanisms driving the DAE precede those driving direction repulsion.

Our second series of experiments tested this hypothesis directly by determining which directions in a bidirectional adaptor, the actual or perceived, induce the direction aftereffect. If the DAE precedes direction repulsion, then the perceptual distortion of a single-direction test stimulus would be driven by the actual adaptor directions. Otherwise, the perceptual distortion should be driven by the perceived adaptor directions. The data from this experiment were consistent with the former scenario.

The combined results of these experiments provide compelling evidence that the DAE precedes direction repulsion in the motion processing hierarchy; and, consequently, they are expressions of processing at different neural sites. Thus, although spatial and temporal contextual interactions in sensory coding may serve a common functional role (Schwartz & Dayan, 2007), in the motion pathway at least they are mediated by different substrates of the processing hierarchy.

The finding that direction repulsion and the DAE are expressions of different neural substrates makes an important contribution to the current debate on the neural location of these phenomena. Kohn and Movshon (2004) report that changes in tuning functions of directionally-sensitive neurons in macaque MT, but not V1, are consistent with perceptual distortions experienced with the DAE; suggesting that the DAE may occur at the global motion level. However, Kohn and Movshon note that their data can also be modelled by

weakening feedforward input from V1 into a recurrent model of MT circuitry; which would be consistent with a local motion processing account of the DAE. Recent psychophysical data pointing to the DAE being a local motion phenomenon (Curran *et al*, 2006a) support the latter interpretation.

In the case of direction repulsion, two studies (Gruenwald, 2004; Wiese & Wenderoth, 2007) found that the phenomenon fails to exhibit interocular transfer, suggesting it to be monocular in origin. Because monocular-driven cortical neurons do not exist beyond area V1, the findings support the notion of direction repulsion being driven by local motion detector activity. However, it should be noted that both studies used very sparse dot stimuli to avoid binocular rivalry (binocular rivalry describes how, when presented with different information to each eye, the different retinal inputs arriving at the cortex compete to dominate perception). Kim and Wilson (1997) avoided this rivalry problem by presenting a central test stimulus to one eye and a surrounding inducing stimulus to the other. They found robust interocular transfer of direction repulsion with this centre-surround configuration. Furthermore, the fact that the effect persisted for non-overlapping moving patterns suggests that direction repulsion may occur after the pooling of local motion measurements. Benton and Curran's (2003) finding that global-motion interactions play a major role in driving direction repulsion support this position.

While data from the experiments reported here do not directly identify where in the motion pathway the DAE and direction repulsion occur, they compellingly illustrate that 1) the two phenomena are expressions of different neural substrates, and 2) the DAE occurs earlier in the motion pathway than direction repulsion. Taken within the context of previous studies, our data are consistent with the DAE occurring at the local motion processing stage, and direction repulsion being driven by neural activity at the global motion processing stage.

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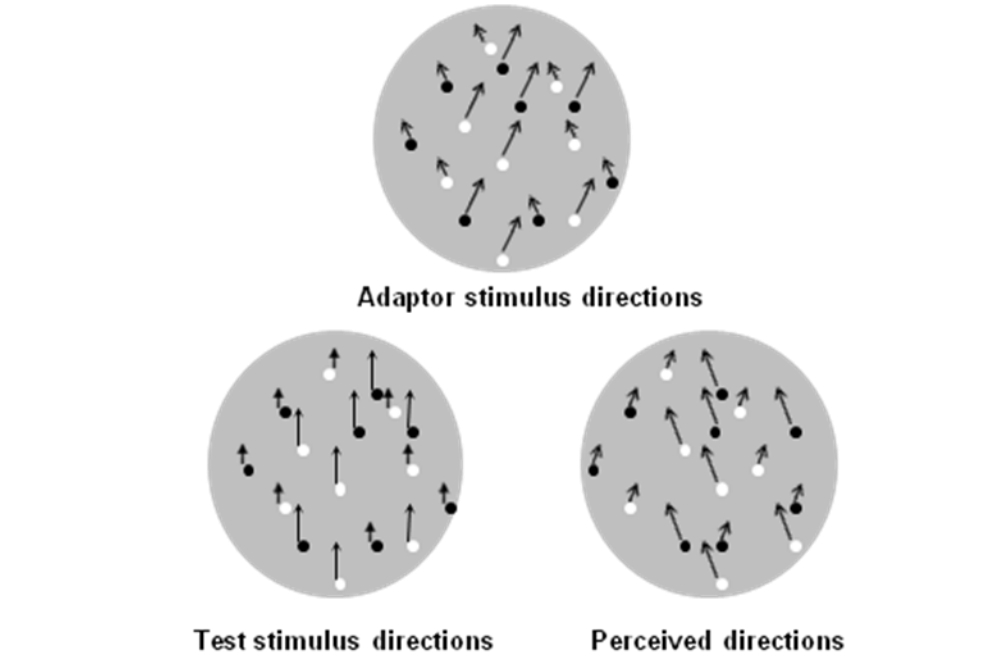
Figure Legends

Figure 1. Direction adaptation affects direction repulsion. **Top:** Depiction of the binary direction aftereffect. Observers adapt to a transparent stimulus containing fast and slow dots moving to the right and left of vertical, respectively. When followed by a test stimulus containing fast and slow dots moving vertically, the fast and slow dots appear to move left and right of vertical, respectively. **Bottom:** Grey bar plots magnitude of the binary direction aftereffect. Black bar plots combined DAEs for single-speed test stimuli, indicating that the binary direction aftereffect contains an additional direction repulsion component. White bar plots the additional direction repulsion. Error bars denote ±1 SEM.

Figure 2. Direction repulsion does *not* affect direction adaptation. **Top left:** The adaptor contained two groups of superimposed dots whose direction differed by 60º (blue arrows). Observers judged the direction of a single-direction test stimulus (red arrow) set halfway between one of the adaptor directions and its perceived direction. **Top right:** Example frame from the Laplacian of Gaussian dot stimuli used in experiment 2. **Bottom:** For all but one observer, perceived direction of the test stimulus (black squares) is closely predicted by the mean DAE of the adaptor's physical directions (blue triangles), indicating that the DAE is driven by the adaptor's actual, rather than perceived, directions.

Figure 1 (Curran, Clifford, & Benton)



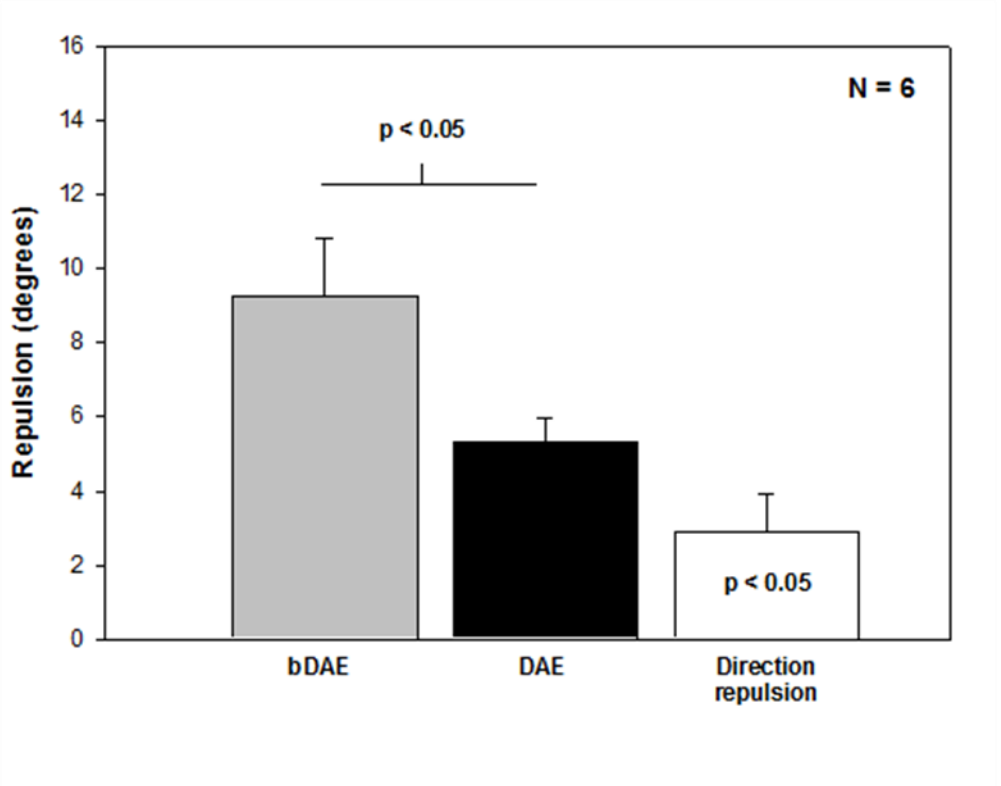


Figure 2 (Curran, Clifford, & Benton)